

THE *LUPINUS MONTANUS* COMPLEX OF MEXICO AND CENTRAL AMERICA¹

DAVID B. DUNN² AND WILLIAM E. HARMON³

ABSTRACT

The recognition of the *Lupinus montanus* complex by morphological traits is discussed. Ecological modification of traits is discussed and the island nature of distribution from mountain peak to mountain peak produces semi-isolated gene pools. Long range dispersal and introgression from other lupines has occurred at the northern end of the distribution in San Luis Potosí, Mexico, developing *L. cacuminus*. A similar situation occurred in Costa Rica, with *L. valerioi* the product of introgression from, as yet, an unknown taxon. In Guatemala var. *austrovolcanicus* represents local introgression from *L. kellermanianus*, into *L. montanus*. Both of the Peruvian (*L. praestabilis* and *L. proculaustrinus*) taxa are, likewise the result of long range dispersal and introgression. The geographic range of each of the taxa of the complex is plotted and the interrelationship is discussed. The alkaloids have been plotted from random samples of each of the taxa and the data supports the taxonomic treatment and interpretation of their interrelationship.

The lupines of Mexico have never been studied monographically. Previous studies have been floristic for states or regions or miscellaneous descriptions, as contributions to the flora of Mexico. To avoid further nomenclatural complications, the earliest named taxa should be identified first. In this sense, the first taxon named for Mexico was *Lupinus mexicanus* Cerv. ex. Lag. (1816), which has been identified (Dunn, 1972). *Lupinus montanus* H.B.K. (1823) was the second epithet published for Mexico, concurrently with *L. elegans* H.B.K. (Humboldt et al., 1823: 478). Both of the types of these taxa are available at Paris, France, with microfiche illustrations now widely distributed. The topotype material was studied and dissections of 50 collections, representing the geographic range of *L. montanus* were made, and the mean measurements were used to prepare the illustrations of *L. montanus* and allies presented in this paper. The illustration of *L. montanus* was sent to Paris and the curator of the herbarium kindly verified that the illustration accurately represents the species by matching it with the type specimen. Since *L. elegans* H.B.K. is the first epithet in a different complex of lupines, it will be treated, as soon as the rest of the complex is understood. With this approach it is believed, after ten years of study of the Mexican lupines and dissection of over 100 types for Mexico, that the taxonomic treatment of the *L. montanus* complex for Mexico and Central America can be presented. C. P. Smith (1948: 608) reported two South Ameri-

¹ The authors wish to express appreciation to the multiple curators of herbaria who loaned material for the study, as cited in the distributions by the code letters from *Index Herbariorum* (Holmgren & Keuken, 1974). Special appreciation is expressed to the curators at Paris for comparing the illustration prepared for *L. montanus* with the type specimen. Two additional herbaria are cited which were not in the code. CUN = University of Northern Colorado, Greeley, Colorado, U.S.A., and WUP = Wisconsin University-Platteville, Platteville, Wisconsin, U.S.A.

² Division of Biological Sciences, University of Missouri-Columbia, Columbia, Missouri 65201.

³ Department of Biology, University of Northern Colorado, Greeley, Colorado 80631.

can species to belong to what he interpreted as the "*Lupinus montanus* complex." Only one of these was available for study. It is a member of the complex and is very distinctive in multiple characteristics. Both are only treated in the key.

MORPHOLOGICAL RECOGNITION

Lupinus montanus, *per se*, can be readily identified by the large sheathing stipules, the largest per specimen being 3–33 cm long. The infraspecific taxa show various modifications of the shape, size, texture, and vestiture of the stipules. (The allies are so different that they cannot be recognized by the stipules.) The stems, 0.5–2.5 m tall (to 4 m shrubs in Peru), are clustered from a woody caudex, and in age become short woody trunks, to 5 cm diameter. The current year's growth is normally hollow and fistulose or subfistulose, varying from 5–30 mm in diameter. (Allies and products of introgression have woody, solid stems, as small as 3 mm in diameter, and are only 3–7 dm tall.) The leaves show no general relationship other than a tendency to have many (9–17) leaflets, palmately compound, linear-elliptic to oblanceolate and generally glabrous above, but the last trait is modified by increasing hairiness above, with higher elevations and by introgression from the allies. The flower structure shows the greatest degree of uniformity, with only very subtle changes in size, shape and vestiture of the calyx, and size and position of the bracteoles. Keels are generally glabrous but both infraspecific taxa and the allies may have ciliate keels. The base of the deep sulcus of the banner appears to have a nectary, which is uncommon in *Lupinus*. The number of ovules varies from taxon to taxon, with *L. montanus* and the infraspecific taxa varying from 7–13 per pod (the allies less). The seeds of *L. montanus* and the infraspecific taxa are very similar in shape to those of *L. polyphyllus*, a species distributed from southern California to British Columbia, with which it has been confused. The seeds are generally 4.5 mm long and 3 mm wide, with a deep funicular pit at the side of one end.

While the large stipules represent the most distinctive trait of the *L. montanus* complex, they are very small in some of the allies and reduced in taxa considered to be products of introgression. The large flowers with the banners reflexing near the midpoint are perhaps the most consistent character of the complex. They may indicate the utilization of specific pollinators.

HABITAT AND ECOLOGICAL MODIFICATIONS

The taxa of the complex are associated with the upper forest openings extending upward to timberline. Thus the population on each mountain represents a breeding population with a chance for some genetic drift or fixation. This is reflected by variations in the hair type from mountain to mountain. However, to view the population on each mountain as having achieved some taxonomic status would be an exaggeration. It appears probable that migratory birds contribute to the separated populations of each mountain peak intermittently. There is also an altitudinal modification of the density of pubescence of both the stems and leaflets. On Popocatepetl the smallest specimens were at the lowest altitude

and the area above timberline. The largest specimens were within the upper margins of timber. The densest pubescence was at the highest elevation and the sparsest pubescence was at the lower elevation, with the leaflets glabrous above at the lower elevations. On Nevada de Toluca, the type locality, the situation was similar. Sharma (1967, in an unpublished part of his thesis) demonstrated experimentally that hair frequency increased with aridity and heat. The vegetative stature of the plants within the complex ranges from 0.3–2.5 m in height, while those within *L. montanus* vary from 0.5–2.5 m tall.

EVOLUTION AND GEOGRAPHICAL RELATIONSHIPS (FIG. 1)

Lupinus muelleri and *L. kellermanianus*, treated here as allies, can be utilized to illustrate both the islandlike mountain isolation and long range disjunction of taxa with morphological similarities. The two are very closely related, but *L. kellermanianus* is known only from two volcanic peaks in Guatemala, while *L. muelleri* is known only from the opposite end of the distributional range of the complex on Cerro Potosí, Nuevo León, Mexico. Vegetatively they are very different from the rest of the *L. montanus* complex, having woody stems, low (3–5 dm) stature, only 2–2.5 cm long petioles, only 2–2.5 cm long leaflets with strigose-sericeous pubescence on both sides, and only 8–20 mm long stipules. The flowers, however, are very similar to *L. montanus* except that both are pubescent on the back of the banner. The vegetative traits, except pubescence, resemble *L. argenteus* of the Rocky Mountains of the United States but the closest geographic approach of this species is in northern New Mexico, while *L. muelleri* occurs in southern Nuevo León and disjunctly in Guatemala, where *L. kellermanianus* also occurs. The pubescence of the leaflets and the banner resembles that of the *L. sericeus* complex, but the closest approach of this complex is in northern Arizona, north of the Grand Canyon. If the source of the characteristics is from the above two complexes of the United States, then long range dispersal seems the only plausible explanation, via migratory seed-eating birds. *Lupinus muelleri* is on a mountain ridge surrounded by Chihuahuan desert, but inhabits the lower pine zone. *Lupinus kellermanianus* was collected high on Volcán Agua near timberline, hence both are in somewhat xeric situations where abundant pubescence is adaptive.

INTROGRESSIVE HYBRIDIZATION

Lupinus cacuminus is vegetatively intermediate between *L. muelleri*, with which it has geographic proximity, and *L. montanus*, from which it is geographically completely isolated. *Lupinus cacuminus* has intermediate stipules, leaflets, and petioles, the fistulose stems of *L. montanus*, but the pubescent banner of *L. muelleri*, and extends above timberline, an ecological trait of *L. montanus*. In some populations of *L. cacuminus* an intermediate amount of ciliation occurs on the keel, a trait derived from *L. muelleri*. The multiple collections are very similar and appear to be a stabilized entity, derived from the hybridization of the *L. montanus* genome with the *L. muelleri* genome. The alkaloid spectrum of *L. cacuminus* is identical with that of *L. montanus* as shown below.

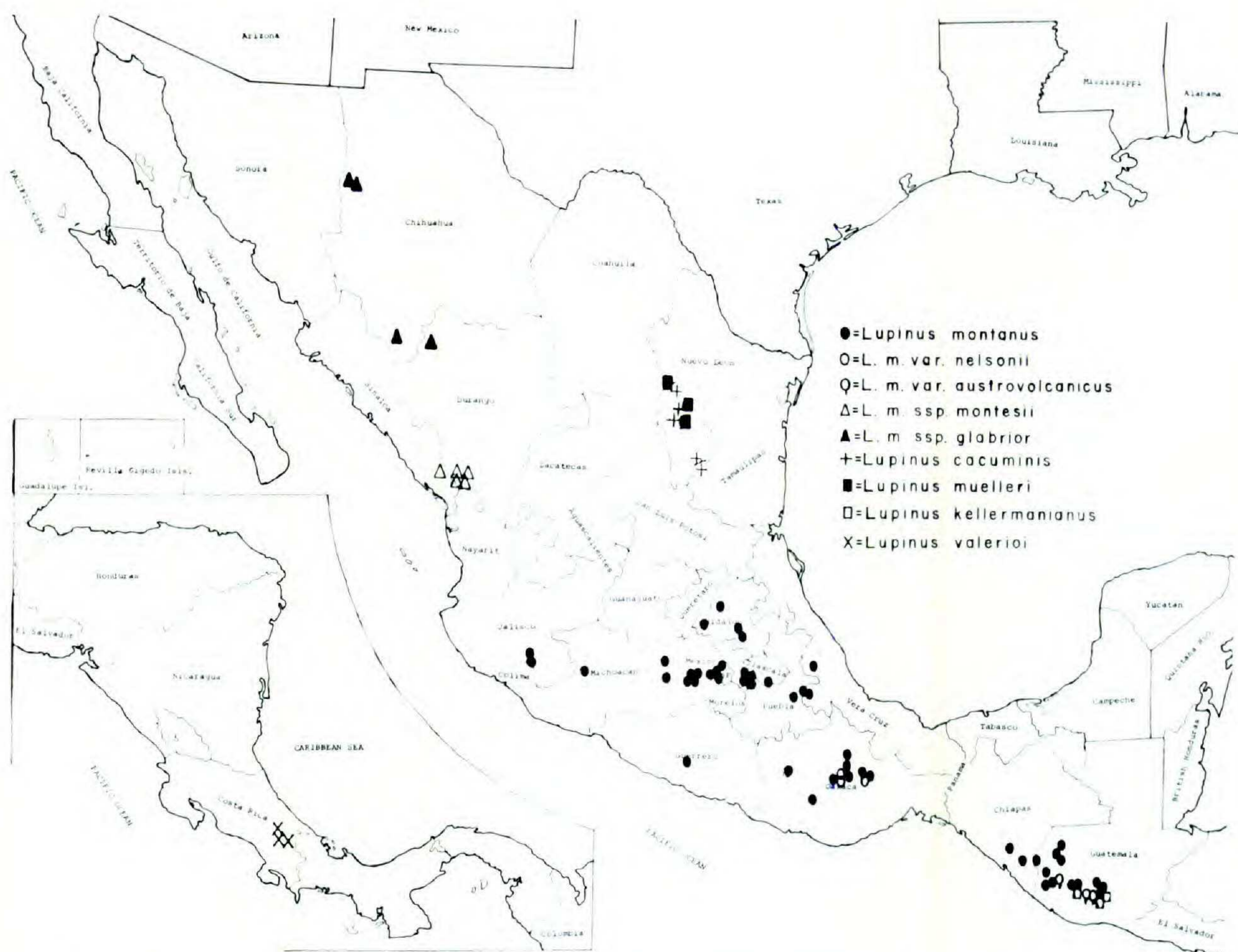


FIGURE 1. Distribution of the taxa of the *Lupinus montanus* complex and their allies in Mexico and Central America.

Lupinus montanus subsp. *montanus* var. *austrovolcanicus* may be the product of introgression between ancestral *L. montanus* and *L. kellermanianus*. In this case *L. kellermanianus* could have provided the woody stem, reduced stature, and intermediate vegetative traits. Both *L. kellermanianus* and *L. montanus* var. *austrovolcanicus* are limited to one or two mountain peaks and have only been collected a few times. It is thus questionable whether the process of introgression has progressed long enough to have established a stabilized taxon of intermediate appearance.

Another possible example of a long range introduction of some portion of the *L. montanus* genome into a lupine population is provided by *L. valerioi* on Cerro Vueltas in Costa Rica. There is a long distance between this population and the nearest known material of *L. montanus* in Guatemala. In this case the stipules are intermediate in size, somewhat similar to those of *L. cacuminis*. The bracts, however, are quite large and broad, typical of *L. montanus*. The stems are very slender, similar to those of *L. kellermanianus*, but the petioles are long, 6–12 cm, and have spreading pilose hairs to 4 mm long. These traits all suggest a mixing of genetic traits of *L. montanus* with some, as yet undetermined taxon of *Lupinus*. None presently known from Costa Rica provides these characteristics.

A fourth example of long range introduction of genetic material from the

L. montanus genome is provided by *L. proculastrinus* C. P. Smith of Peru. In this case the plants have retained many of the traits of *L. montanus*, including the large sheathing stipules and large broad bracts. The species has multiple unique traits, however, which are not present in *L. montanus*. A conspicuous one is the glabrous, glaucous surface and also a shrubby stature, reported on some specimens to be up to 4 meters in height. The other Peruvian species, *L. praestabilis* C. P. Smith has not been available for study.

ALKALOID CHEMISTRY

The material utilized was dried leaflets in all cases, since we have observed some cases where the alkaloids stored in the seeds were different from those present in the leaves. Seed material is not always present. Four to five leaflets were fragmented in a new coin envelope for each sample and transferred to a test tube. In species with large leaflets only one is necessary. Enough 30% KOH was added to wet the leaf fragments. Enough chloroform was added to cover the fragments. The rack with the test tubes was then stored in a refrigerator for one day (24 h). A micropipette was utilized to spot 50 μ l of the clear chloroform solution from the bottom of the test tube, for each sample, onto a thin-layer chromatographic plate (TLC). If no clear bottom layer was present, a few drops of chloroform was added to the test tube. The solvent utilized to separate the alkaloids was 95 parts chloroform, 4 parts anhydrous methyl alcohol, and 1 part ammonium hydroxide, by capillary flow, against gravity, in a Brinkman tank. The flow was stopped at 15 cm and the plate dried and developed first with Dragendorff's reagent. All visible spots were marked with a pencil. The plate was then sprayed with iodoplatinate to bring out any trace substances not observed with the first stain. The R_f values plotted in Table 1 have been correlated with standards supplied by Cho & Martin (1971) for sparteine, lupanine, hydroxylupanine and cytisine, on each plate that was prepared.

While the number of samples plotted is not large, it is quite clear that while some variation occurs in the trace alkaloids, the presence of the principal alkaloids is fairly consistent. Within *L. montanus* both varieties retain the same principal alkaloids, while the two subspecies show distinct alterations in the principal alkaloids. The suggestion that *L. kellermanianus*, *L. valerioi*, and *L. cacuminus* are allied is supported by the fact that the samples analyzed show the same principal alkaloids as those in *L. montanus* proper.

Lupinus muelleri has a distinctly different spectrum of alkaloids from *L. cacuminus* suggesting that the two taxa are maintaining their isolation at the present time, even though they are in close proximity and are separated only altitudinally by a few hundred feet.

The lone specimen available from Volcán Colima, probably in Jalisco, suggests that this population may be sufficiently isolated to require recognition. However, a single sample is not sufficient to permit an analysis of the situation, particularly since it appears to be morphologically very little different from the main population of *L. montanus*, even though it is geographically isolated.

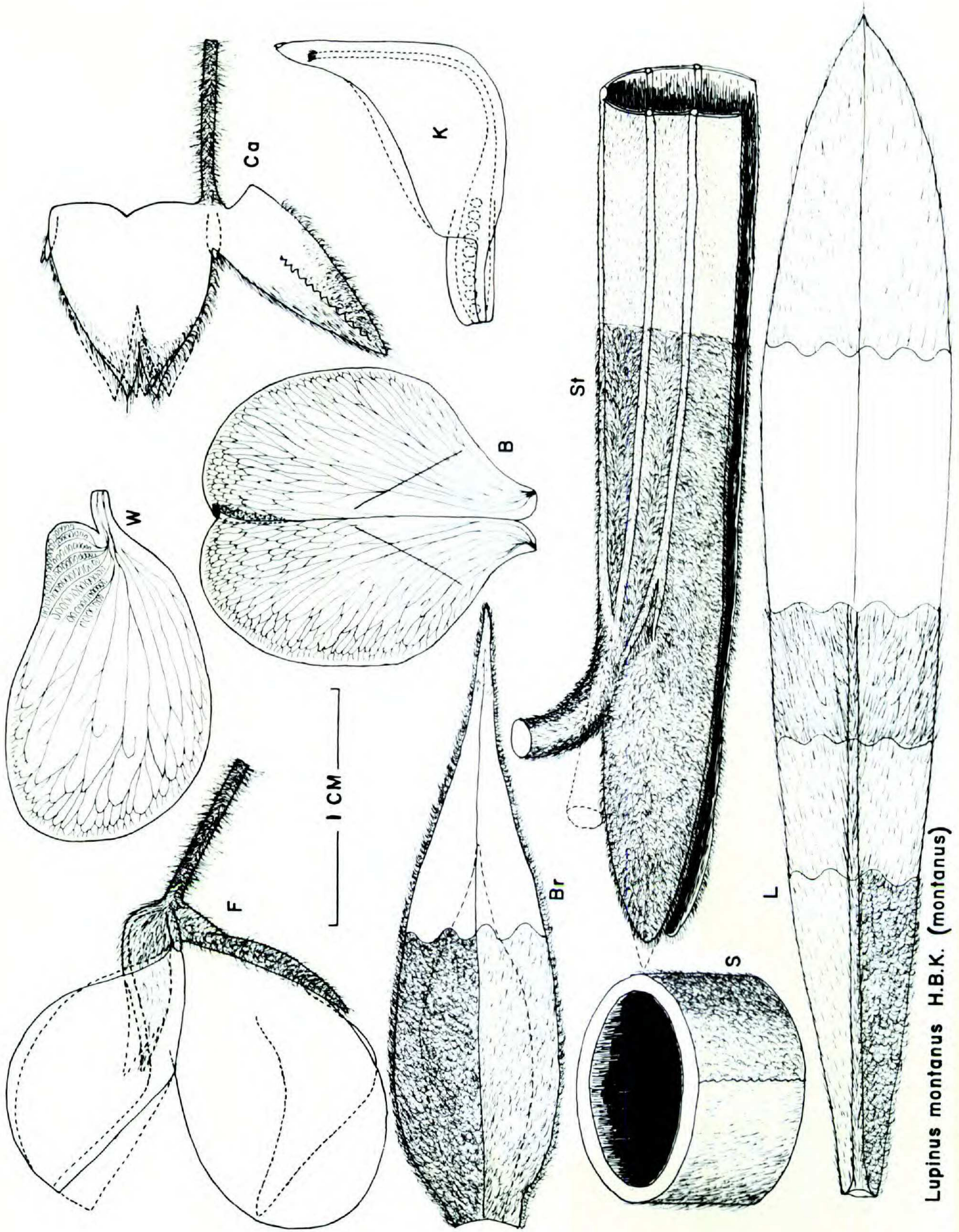
TAXONOMY

KEY TO *Lupinus montanus* AND ALLIES

- a. Banner sparsely strigose dorsally, near the distal half, along the crest; stipules 4.5 cm long or less (see also var. *australovolcanicus*); leaflets linear to linear-lanceolate, 2.5–5 cm long, strigose to sericeous above.
- b. Plants about 14 dm tall or more, glabrous or minutely puberulent; bracts persistent; known only from Peru (not treated) *L. praestabilis*
- bb. Plants 4–9 dm tall, sericeous to strigose; known from Guatemala or Mexico.
- c. Petioles 5–13 cm long; stems hollow, fistulose below; pubescence appressed-sericeous; Nuevo León, Mexico 2. *L. cacuminus*
- cc. Petioles 2–4.5 cm long; stems solid and ligneous.
- d. Keels glabrous; pubescence of leaflets strigose-sericeous; known from Guatemala 4. *L. kellermanianus*
- dd. Keels ciliate; pubescence of leaflets strigose-sericeous; known from Coahuila and Nuevo León 3. *L. muelleri*
- aa. Banner glabrous; largest stipules more than 4.5 cm long or the stems with long spreading pilose hairs, 3–4 mm long; leaflets mostly glabrous above, sometime strigose above, variable in size up to 15 cm long.
- e. Pubescence of the stems with abundant spreading pilose hairs to 4 mm long; stems becoming ligneous; petioles 6–12 cm long; largest leaflets 4–7 mm long; known from Costa Rica 5. *L. valerioi*
- ee. Pubescence of the stems strigose, glabrous, or canescent; petioles variable in size; stems ligneous or herbaceous; largest leaflets 5–15 cm long; widely distributed.
- f. Stems and stipules glabrous to minutely puberulent; leaflets glabrous above; keels glabrous or sparsely ciliate above distally; known from Chihuahua, Durango, or Peru.
- g. Stems glabrous and glaucous; flowers 18–20 mm long; shrubs to 3.5 m tall; known only from Peru (not treated) *L. proculastrinus*
- gg. Stems glabrous or glabrate; flowers 15–18 mm long; herbaceous stems 5–15 dm tall; known from northwestern Mexico.
- h. Bracts lance shaped, strigose dorsally; upper lip of the calyx truncate with an irregular notch; known from Chihuahua and northern Durango 1d. *L. montanus* subsp. *glabrior*
- hh. Bracts lanceolate, the tips attenuate and setaceous hairy, the lower dorsal area glabrous; upper lip of the calyx triangular; known from southwest Durango and Sinaloa 1e. *L. montanus* subsp. *montesii*
- ff. Stems, stipules, and bracts abundantly pubescent; known from other areas of Mexico and Guatemala.
- i. Stipules hispidulous to canescent within, the largest 10–33 cm long; stems fistulose, hispidulous to retrorsely hispidulous, 12–33 mm in diameter; known only from Ixtlán, Oaxaca, Mexico 1b. *L. montanus* subsp. *montanus* var. *nelsonii*
- ii. Stipules glabrous within, or if pubescent, not with the above combination of characteristics, generally less than 10 cm long; stems puberu-

→

FIGURE 2. Illustration of the typical structures of *Lupinus montanus* subsp. *montanus* var. *montanus*. The floral and vegetative parts are drawn to the mean value of a set of 30 dissections from the geographic range of the taxon. The lettering is the same on all of the figures: F = lateral view of the left side of the flower; B = banner petal flattened, dorsal view; Br = bract, outside lower portion, inside upper portion; Ca = calyx, cut at the left lateral sinus and opened so that the inside is illustrated; K = keel petals, enclosing staminal tube and pistil, with the mean number of ovules drawn; L = average largest leaflet drawn to ½ the scale used for the floral part, the lower half shows different hair types observed on the lower surface, the upper half shows hair types observed on the upper surface; S = stem structure of first year growth and hair types, half scale; St = sheathing pair of stipules, half scale, showing hair types; W = wing petal.



Lupinus montanus H.B.K. (montanus)

lent to strigose or hispidulous, hollow, 4–12 mm in diameter on the first year's growth, becoming ligneous.

j. Stems to 4 mm in diameter, but hollow on the first year's growth, finely appressed puberulent; stipules only 2–4.5 cm long and pubescent within; racemes generally less than 8 cm long; rare, known from Volcán Santa María, Guatemala

----- 1c. *L. montanus* subsp. *montanus* var. *austrovolcanicus*

jj. Stems of the first year's growth over 5 mm in diameter, hollow and flattening on pressing, variously pubescent; largest stipules 4–9 cm long, commonly glabrous over most of the area within; racemes over 15 cm long at maturity; known from Guatemala to central Mexico ----- 1a. *L. montanus* subsp. *montanus* var. *montanus*

1a. ***Lupinus montanus*** H.B.K. subsp. ***montanus*** var. ***montanus***, Nov. Gen. Sp. Pl. 6:477. 1823. TYPE: Mexico, Montosis Novae Hispaniae (Nevada de Toluca, 9,000–10,000 ft) (P, holotype, not seen; microfiche, MO).—FIG. 2.

L. vaginatus Cham. & Schlecht., Linnaea 5:590. 1830. TYPE: Mexico, Monte Orizaba, Sep., Schiede & Deppe (HAL, holotype; photos, NY, TEX, UMO).

L. flabellaris Bertol., Fl. Guat. 30. 1840. TYPE: Guatemala, Volcán d'Agua (not seen). TOPO-TYPE: Harmon 3646 (MO, NY, UC, UMO, US).

Plants perennial, 0.8–2 m tall, rarely to 2.5 m; stems hollow above the ground level, with the current year's growth 5–12 mm in diameter, pubescence varying with locality and altitude, finely appressed puberulent, to strigose or sericeous, more densely at higher altitudes, or hispidulous to retrorsely hispidulous or canescent; petioles of the primary leaves along the upper stems 6–15 cm long with the stipules connate nearly half the length of the petioles, those of dwarf lateral branches often reduced in size; stipules ensheathing $\frac{3}{4}$ or more of the diameter of the stems, 4–9 cm long, the triangular free tips 4–12 mm long, both petioles and stipules pubescent dorsally as the stems, the stipules generally glabrous or glabrate within, on dwarf branches the stipules of the multiple leaves imbricated; leaflets of the larger primary leaves 10–15, linear to narrowly oblanceolate, the largest 5–13 cm long, 5–14 mm wide, generally glabrous above at lower elevations and puberulent to strigose above at higher elevations, the tips acute or slightly attenuate; peduncles 10–22 cm long, shorter on late-season branches; racemes 15–30 cm long at maturity, verticillate to subverticillate; bracts large-sheathing or covering 3–5 cm of the tip of the elongating raceme, hiding the buds, the tips attenuate-caudate, pubescence as the stipules for each population, generally caducous; pedicels 5.5–8.4 mm long, hispid or with appressed hairs; calyces sericeous, strigose or canescent on the outside, puberulent within on the distal portion of both lips, the lower lip 8–11 mm long, generally entire, the upper lip 5.5–8.4 mm long, the notch at the tip 1–5 mm deep, the lips connate laterally 1.4–1.8 mm, the bracteoles 1.0–3.4 mm long, attached below the lips of the lateral sinuses; corollas glabrous, blue to lavender or purple, occasionally white or pink; banner obovate-rotund, longer than wide, the tip emarginate, 12.6–14.8 mm long, 11–14.5 mm wide, reflexed near the midpoint, reflexed 5.7–8 mm, appressed 6.7–7.8 mm, reflexed/appressed ratio 0.81–1.06, the angle 130°–146°; wings 13.8–16 mm long, 6–10 mm wide, the claw 2–3.7 mm long; keel 4–5 mm wide in the middle, the angle 84°–98° (average 90.9°); ovules 7–10; pods 4–5 cm long, 9–10 mm wide when dried, arching

up and outward, abundantly to sparsely tangled-pilose, the hairs 1–2.5 mm long; seeds black or brown with dark mottling, 4–4.5 mm long, 3–3.6 mm wide, with a deep funicular pit; chromosome number $n = 24$ (Beaman et al., 1962).

This is one of the wide-ranging species of the volcano zone of Mexico and Central America. It occupies a zone on most of the high mountains from timberline, or above in sheltered areas, down through the upper pine forest into the mixed pine-oak forests. The dominant alkaloid produced is sparteine, with only traces of minor alkaloids. Nowacki's (1963) contention that sparteine is the primitive alkaloid would suggest that this may be one of the older, more primitive species of *Lupinus* in North America. The trait of many leaflets and the fistulose stems have caused many botanists to mistake this taxon for *L. polyphyllus* which ranges from California and Oregon north into British Columbia. The huge sheathing stipules, however, make *L. montanus* easily recognizable. While *L. polyphyllus* is considered as one of the older taxa of the West Coast, it has the necessary genes to convert or utilize sparteine, changing it into several other alkaloids. The two northern subspecies of *L. montanus* have also modified genomes so that they concentrate other alkaloids. The presence of what appears to be a distinct nectary at the base of the ventral sulcus of the banner and the thickened glandlike upper surface of the base of the staminal tube seem to be unique in *Lupinus*.

While the original description of *L. montanus* failed to mention the sheathing stipules, they are clearly recognizable in the microfiche of the type specimen, and the material from Mt. Orizaba differs from that of Nevada de Toluca only in the hair type being hispidulous to canescent, hence the contention that *L. vaginatus* is a synonym. The type description of *L. flabellaris* clearly mentions the sheathing stipules and topotype material is indistinguishable from the Mexican portion of the taxon, both morphologically and chromatographically.

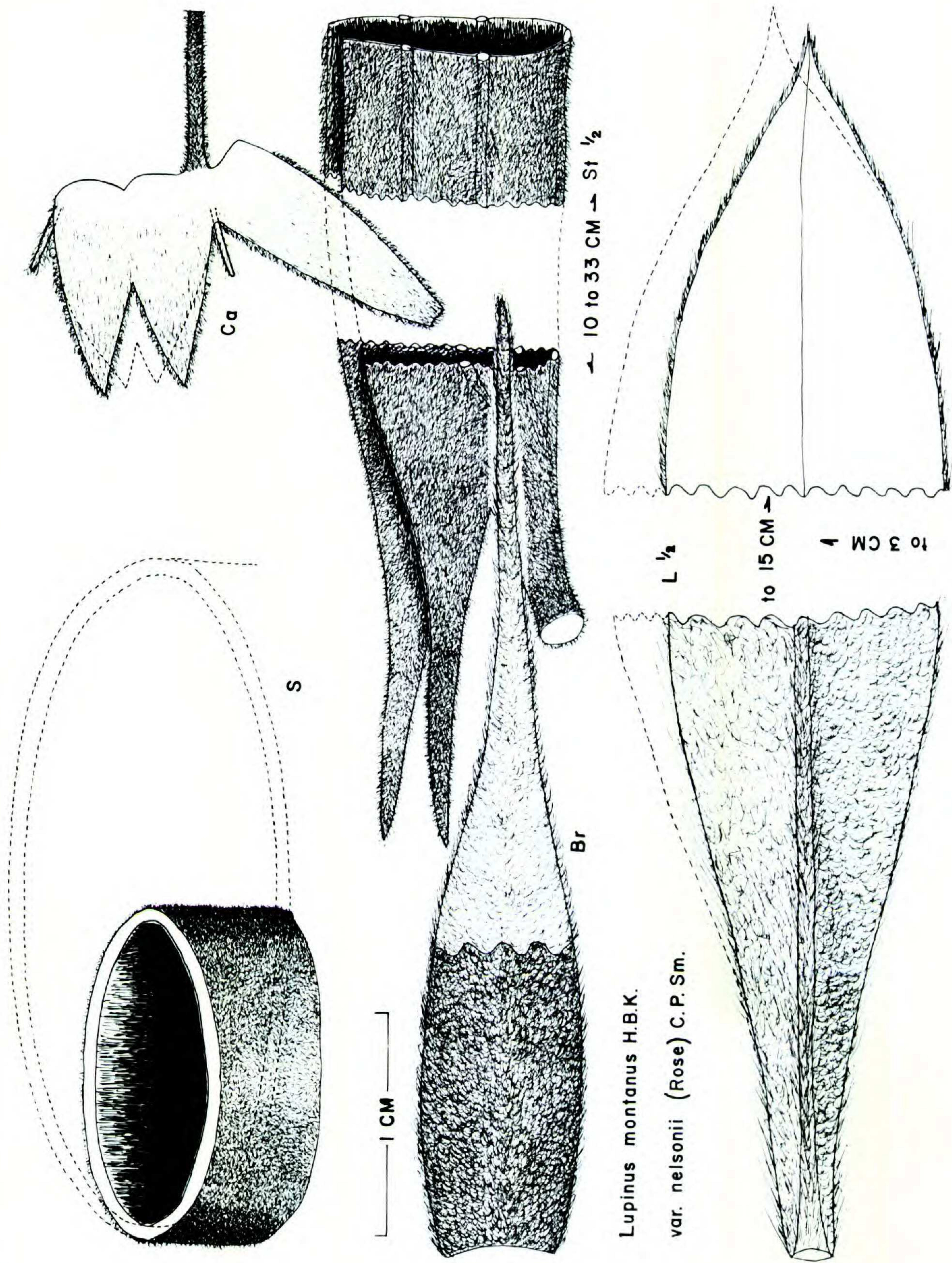
GUATEMALA. DEP. CHIMALTENANGO: Chichavac, *Skutch* 107(US). Chichoy Pros, *Hunnell* 17145(GH). San Marcos, *I. R. Johnston* 1229(F). Sierra San Elna, *Siler* 2303(GH). Volcán Acatenango, *Beaman* 3258(GH, MSC, TEX, US); *Standley* 61902(F). Volcán de Agua, *I. R. Johnston* 578(F). Volcán Fuego, N side, *Beaman* 4025(GH, MSC, US). DEP. HUEHUETENANGO: Cumbre Papal, *Steyermark* 50945(F). Between Tocquia and San Juan Ixcay, *Moncure* in 1950 (F). Between Tunima and Quisil, *Steyermark* 48426(F). DEP. QUEZALTENANGO: Canton La Eseranza Forest, 6 km from San Juan Ostuncalo, *Molina et al.* 16648 (F, US). Cerro Lieteoreya, *Koninck* 302(US). 10 mi W of Quezaltenango, *King* 3199 (MICH, TEX, US). 11 mi SE of San Marcos, *King* 3173(MICH, TEX, US). Sierra Madre Mts., *Williams et al.* 22780(F, US, WIS), 22800(F). Volcán Santa María, *Skutch* 855(F, GH, US); *Steyermark* 34168(F). Volcán Santo Tomás, *Steyermark* 34857(F). DEP. SACATEPÉQUEZ: Volcán Agua, *Harmon* 3598(UMO, US, WIS), 3646(CAS, CUN, F, MICH, MO, UC, UMO, US); *Beaman* 2942(GH, MSC, TEX, US); *Kellerman* 4708(US); *Maxon & Hay* 3687 (US); *Molina* 21029(F); *Salas* in Jan. 1926(US); *Shannon* 3679(US); *J. D. Smith* 2152 (US); *Standley* 65093(F). DEP. SAN MARCOS: Cerro El Bonito, *Plowman* 5044(GH). Between San Sebastian and summit, *Steyermark* 35553(F); summit, *Steyermark* 35530(F). 2 mi S of San Sebastian, *Williams et al.* 25915(F, WIS). Volcán Tacaná, *Beaman* 3230(GH, MSC, TEX, US); *Steyermark* 36140(F). Volcán Tajumulco, *Beaman* 3140(GH, MSC, TEX, US); *Reeder* in Apr. 1952(MICH); *Shannon* 568(US); *Williams et al.* 26996(F, GH, US). DEP. SOLOLA: Volcán Atitlán, *Beaman* 4094(GH, MSC); *Kellerman* 5769(US); *Steyermark* 47508(F, US). Volcán Santa Clara, *Steyermark* 46988(F). Volcán Tolimán, *Steyermark* 47535(F). DEP. TOTONICAPÁN: Cerro María Tecúm, *Williams et al.* 23145(F). Boundary of Depts. Huehuetenango and Quezaltenango, *Williams et al.* 22707(F, GH, US, WIS). Los

Encuentros y María Tecúm, *Molina* 15879(F, US, WIS). 8 km S of Totoncapán, *Williams et al.* 22941(F, US); *Lind* 11(V, WIS).

MEXICO. CHIAPAS: Mt. Pasitár, *Matuda* 70(MICH, NY, US); *Matuda* S-209(MICH). Volcán Tacaná, *Matuda* 2333(GH, MICH, WIS). COLIMA: Cuchilla, Nevada de Colima, *Goldsmith* 57(F, GH, MO, US). DISTRITO FEDERAL: Cerro Ajusco, *Beaman* 2796(GH, MSC, US); *Garcia* in May 1954(IPN). Pedregal de San Angel, *Barclay & Paxton* 530(F, TEX). Peña de los Charros, *Russell & Souviron* 139(US). GUERRERO: Mina, Cerro Teotepec, *Hinton* 14266(GH, MICH, US); *Rzedowski* 16493(ENCB, MICH). HIDALGO: Plains of Actopan, *Graham* 168(GH). Cerro de las Venturas, N of Pachuca, *Galvan* in Aug. 1963 (ENCB); *Nuñez* 56(UMO). El Chico, *Dunn et al.* 20298(UMO, US). Sierra de Pachuca, *Rose & Hay* 5628(US); *Pringle* 9530(F, GH, MO, US, VT). JALISCO: Nevada de Colima, *Beaman* 2366 (MICH, MSC, US); *Matuda* 38369(MEX, UMO); *McVaugh* 10076(MICH, small flowers). MEXICO: 10 km E of Amecameca, *Quijana* 51(ENCB). 11 mi E of Amemeca, *Dodds* 11 (MICH); *Montgomery & Root* 8114a(MSC). Cerro Jocotitlán, *Matuda* 38490(MEX, UMO). Crucero? Agua-Blanca, *Hinton* 8244(GH), 8317(GH, MO, RSA, UMO, US). Crucero-Raices, *Hinton* 9031(F, GH, ENCB, MO, RSA, UMO, US). Estacca, *Matuda* 38503(MEX, UMO). Ixtachuatl, Falda, *Matuda* 26148(NY, US); *Beaman* 3477(GH, MSC, US, $n = 24$); *Nelson & Goldman* in Jan. 1894(US); *Purpus* 32(US), 203(MO); *Rudd* 1029(UMO, US); *Rzedowski* 19806(ENCB, UMO). Mesón Viejo, *Matuda* 38395(MEX, UMO). Nevada de Toluca, *Balls* 4088(US); *Dunn* 18837(UMO), 18840(ENCB, MSC, MO, NY, TENN, UMO, US); *Dziakowski et al.* 1915(MEMO, MO, NY, UC, UMO, WUP), 1932(ASU, GH, MO, MSC, OSC, SLP, TENN, UMO), 1936(MEMO, MO, RSA, UMO, US, WUP); *Gallian & Leake* 897 (UMO); *Galliotti* 3360(P); *Hunnewell* 13146(GH); *Islas* 28(MEMO); *Mick & Roe* 187 (ENCB); *Morales-Diaz* in Aug. 1962(ENCB); *Rose & Painter* 7906(US); *Rzedowski* 15782 (ENCB); *Schery* 90(MICH, MO, US). Paso de Cortez, *Iltis et al.* 1025(MICH, MSC, TEX, WIS). Pesco Inst. de Nacional, *Dunn et al.* 20373(F, GA, K, ENCB, MEMO, MO, NEL, NY, ORE, RSA, UC, UMO, US, WUP). Río Frio, *Contreras* in July 1962(ENCB). Tlamacas, vic. of Popocatepetl, *Fonseca* F5(ENCB); *Galicia* in July 1962(ENCB); *Garcia* 3A(ENCB); *Lundell* 12358(MICH, TEX); *Madrigal* in Dec. 1959(ENCB); *Matuda* 38497(MEX, UMO); *Moore* 36(GH); *Quijano* 51(ENCB). Volcán Popocatepetl, *Balls* 4227(US); *Barkley et al.* 2353(TEX); *Beaman* 2022(MSC); *Dunn* 18566(UMO); 18579(CUN, ENCB, MO, NY, UMO, US); *Galliotti* 3368(P); *Hatheway* 1193(GH, MO, US); *Huerta* 101(ENCB); *Leake & Gallian* 133, 141(UMO); *Lundell* 12358(US); *Rose & Hay* 6012(US); *Ross* 8(US); *Straw & Gregory* 1003(GH, MICH, RSA). MICHOACÁN: Cerro San Andres, 12 km N of Hidalgo, *Beaman* 4295(GH, MSC, TEX, US). Mt. Tancitaro, *Hinton* 15593(US); *Leavenworth & Hoogstraal* 1128(F, MO). Zitácuaro-Cacique Peak, *Hinkson* 11932(US). OAXACA: Atepec, Llano de las Flores, *MacDougal* 378.S(NY). Cerro de San Felipe, *Camp* 2869(NY). Cerro Zemoaltepetl, *Hallberg* 790(ENCB, MICH, US). Cumbre de Sierra de Juárez, *Matuda* 38415(MEX, UMO). Gueletago, *Vilas* 31(WIS). 27 mi N of Ixtlán, Sierra Juárez, *Roe & Roe* 1941(ENCB, MICH, WIS). Macuiltianguis, *MacDougal* in 1960(US). Mt. Zemoaltepec, summit, *E. Nelson* 619(US). Reyes, *E. Nelson* 1736(MICH, US). Sierra de Ixtlán, *Gentry et al.* 20272(UMO). Sierra Madre del Sur, 60 mi NE of Oaxaca, *Webster* 11543(MO). Sierra de San Felipe, *Camp* 2869(NY); *E. Nelson* 1135(US); *Pringle* 4779(F, GH, ISC, MICH, MSC, ND-G, P, US, VT); *C. L. Smith* 333(MO). PUEBLA: Iztaccihuatl, *Beaman* 2007(GH, MSC, US); *Iltis et al.* 1025(TEX); *Weber* 372(ENCB). Pass between Mexico City and Puebla, *Mexia* 2647(MICH), 2647A(CAS). Alberque Piedra Grande, *Beaman* 3640(GH, MSC, TEX). Ciudad Serdán, *Beaman* 2498(GH, MSC). Pico de Orizaba, *Gelliotti* 3343(P); *Greenman* 28(F); *Liebman* 4892(F, GH), 4893(F); *Pringle* 9528(F, GH, MO, US, VT); *Schiede* 666(HAL; photos, GH, TEX, UMO, US); *Seaton* 510(GH). Popocatepetl, *Barkley* 17Mo87(F); *Barkley et al.* 2353; *Beaman* 1747, 2109(GH, MSC); *Dunn* 18558(UMO), 18564(CUN, ENCB, MO, NY, UMO, US); *Miranda & Barkley* 17Mo87(TEX, MSC). TLAXCALA: Mt. Malinche, *Balls* 4890(US). VERACRUZ: Cerro de Perote, *Balls* 4604(US). Cueva

→

FIGURE 3. Structures of *Lupinus montanus* subsp. *montanus* var. *nelsonii* drawn to mean values, for those traits which differ from var. *montanus*. The calyx, bract and stem are drawn to the scale shown, while the stipule and leaflet are half scale. The lettering is Br = bract; Ca = calyx, inside view; L = leaflet; S = stem; St = stipules. (See legend for Fig. 2 for full explanation.)



Lupinus montanus H.B.K.
var. *nelsonii* (Rose) C. P. Sm.

de Muerto, *Beaman* 1783(MSC, US). Pico de Orizaba, *Beaman* 2291(MSC); *E. Nelson* 266(US); *Rose & Hay* 5727(US); *J. G. Smith* 391(MO). Unknown locality, *E. Nelson* 38(US).

1b. ***Lupinus montanus*** subsp. ***montanus*** var. ***nelsonii*** (Rose) C. P. Smith, *Sp. Lup.* 79. 1938.—FIG. 3.

L. nelsonii Rose, *Contr. U.S. Natl. Herb.* 8:308. 1905. TYPE: Mexico, Oaxaca, near Cerro de San Felipe, *E. W. Nelson* 1145(US, holotype, photo, UMO).

Differs from *L. montanus* in the large fistulose stems, up to 3 cm or more in diameter, the fistulose nature extending throughout the above ground portion to the top of the raceme; plants to 2.5 m tall; stems densely hispidulous to retrorsely hispidulous; petioles to 50 cm long; leaflets 15, to 15 cm long and 3 cm wide, pilose to canescent below and glabrous above; stipules 10–33 cm long, connate to the petioles for all but 1–2 cm at the tip, the free tips slender attenuate-caudate, both stipules and bracts hispidulous-canescant within as well as densely so without; bracts numerous, plumed, the tips elongate-caudate, 3–4.5 cm long, pilose-canescant, as also the under side of the leaflets, the bracts hiding 5–8 cm of the buds at the tips of the racemes, often subpersistent; flowers the same as the species; pods and seeds the same as the species except the pods densely hispidulous.

The taxon appears to be a gigas form and may represent an ecological modification since there are many typical specimens of *L. montanus* in the region. There are distinctive traits, however, which appear to have a genetic basis, and the taxon has been collected on several occasions from 1894 to 1964. It is also chromatographically similar in its alkaloids to other samples of *L. montanus*.

MEXICO. OAXACA: Ixtlán, Atepec, Llanos de las Flores, *MacDougal* 378s(NY). Oaxaca-Tuxtepec Hwy., Llanos de las Flores, *MacDougal* in 1960 (US, 4 sheets). Cerro de San Felipe, *E. Nelson* 1145(US); *Pringle* 5839(GH, VT). Cerro Zemoaltepetl, *Schultes* 502(GH); *Hallberg* 790(MICH, in part). Ixtlán de Juárez, Sierra Ixtlán, *Gentry* 20272(UMO, US). 13 mi N of Ixtlán, *Anderson* 4842(MICH).

1c. ***Lupinus montanus*** subsp. ***montanus*** var. ***austrovolcanicus*** C. P. Smith, *Sp. Lup.* 90. 1938. TYPE: Guatemala, Volcán Santa María, 8,000–11,500 ft, *E. Nelson* 3709(US-250873, holotype; F, GH, isotypes).—FIG. 8.

Plants perennial, over 3 dm tall; stems hollow, ligneous, 4 mm in diameter, finely appressed puberulent; petioles 6–10 cm long; larger stipules 3–4.5 cm long, wide, membranous, sparsely pilose to canescent inside and outside, the free tips 7–11 mm long; leaflets 10–11, linear, acute, mucronate, the longest 5.5–6.5 cm long, 6–8 mm wide, sparsely strigose above, thinly kinky canescent beneath; peduncles 2–8 cm long; racemes ca. 8 cm long, verticillate, the lower whorls to 2 cm distant; bracts ca. 16 mm long below; pedicels 5–6 mm long, slender sericeous-puberulent; calyces canescent without, finely sericeous within near the tips of the lips, the lower lip slender, arcuate, 8–9 mm long, entire, the upper lip ovate, bidentate, 7 mm long, the lips connate laterally 2 mm, the bracteoles 1.5–2 mm long, attached near the lip of the lateral sinuses; banner suborbicular, glabrous or occasionally sparsely hairy on the distal portion of the dorsal crest, 11.5–12 mm long, 11–11.5 mm wide, widest above the midpoint, reflexed 6.7 mm, appressed 7 mm; wings 12.8–13 mm long, 7 mm wide; keel

with minute papillae above the claws, 3.5 mm wide in the middle, the angle 95° – 100° at anthesis; ovules 6–7; pods 3–4.5 cm long, 9 mm wide, pilose with hairs 1–2 mm long.

The specimens seen appear to represent hybridization and introgression from *L. kellermannii*. The slender woody stems, short stature of the plants, narrow smaller leaflets, intermediate petioles, and the presence of pubescence dorsally on the banners of about half of the specimens all suggest introgression. The flower size and stipules are distinctly like those of *L. montanus*.

GUATEMALA. DEP. QUEZALTENANGO: Volcán Santa María, *Beaman 4124*(ENCB, MSC, TEX, US); *E. Nelson 3709*(F, GH, US); *Steyermark 34205*(F). Above Palojunoj, *Standley 67703, 67707, 67738*(F), *67683*(F, intermediate to var. *montanus*).

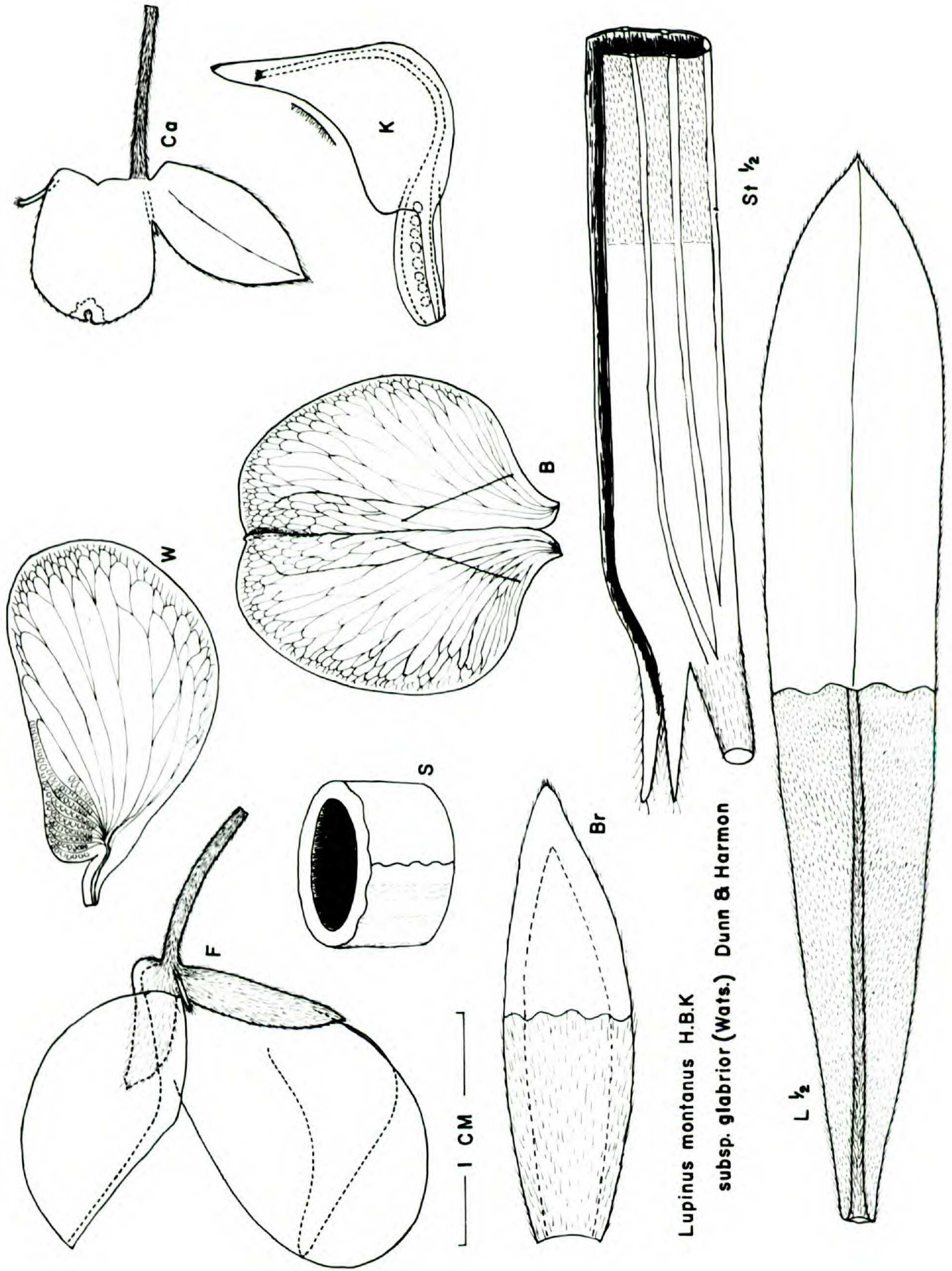
1d. *Lupinus montanus* subsp. *glabrior* (Wats.) Dunn & Harmon, comb. nov.
—FIG. 4.

L. montanus var. *glabrior* Wats., Proc. Amer. Acad. Arts 23:270. 1888. TYPE: Mexico, Chihuahua, summit of Sierra Madre, *Pringle 1206*(GH, holotype; F, G, K, ND-G, P, RSA, US, VT, isotypes; photo, UMO).

L. glabrior (Wats.) Rose, Contr. U.S. Natl. Herb. 8:308. 1905.

Plants perennial, to 1 m tall; stems glabrous to glabrate, ligneous ridged, at least on drying, fistulose, 6–8 mm in diameter; petioles 12–20 cm long, the free portion finely strigose; stipules membranous, sheathing and often imbricate on dwarfed branches, 4.5–6 cm long, the free tips only 3–6 mm long; leaflets 14–15, the largest 9–11 cm long, 12–13 mm wide with acute-mucronate tips, glabrous above, sparsely and finely puberulent below; peduncles to 17 cm long; racemes 20–30 cm long at maturity, verticillate, the lower whorls, 2.5–3 cm distant, the rachis finely but densely puberulent; bracts broadly lanceolate, membranous, gradated, the lower to 2 cm long, the upper reduced, minutely puberulent without, glabrous within; pedicels 6–8 mm long; calyces with broad boat-shaped lips, finely puberulent without, glabrous within, the lower lip 7–8 mm long, entire, the upper lip 5–7 mm long, the apex blunt with an irregular notch 0.5–0.8 mm deep, the lips connate 1.4 mm, the bracteoles straplike, 2–3 mm long, glabrous, except for a few setaceous hairs near the tips; corollas glabrous except for a few papillae above near the claws of the keel or occasionally the keel ciliate above toward the acumen; banner orbicular, 13–14 mm long, 13–15 mm wide, reflexed 7 mm, appressed 6.5–6.8 mm, the sulcus 2.4 mm deep midway between the umbo and the base, the banner angle 133° – 150° ; wings 15–17 mm long, 8–10 mm wide; keel 4–5.3 mm wide in the middle, the angle 80° – 85° , occasionally papillae near the claws or occasionally ciliate above near the acumen; ovules 7–9; pods 8–8.5 mm wide, 3.5–4.5 cm long, thinly strigose; seeds nearly black with mottling, 4.5 mm long, 3 mm wide, a pit at the funicular attachment.

The subspecies *glabrior* is known only from northern Durango and Chihuahua, from the summit of the Sierra Madre Occidental, in rather inaccessible areas. The area is north of that of subsp. *montesii* and subsp. *montanus*, as well as the fact that there are distinctive morphological traits in addition to distinct



Lupinus montanus H.B.K.
subsp. *glabrior* (Wats.) Dunn & Harmon

chromatographic differences. The best distinguishing traits are the short, blunt upper lip of the calyx and the lanceolate bracts. While other traits are distinct, they are not as easily recognized. Since the geography, ecology, morphology, and chromatography suggest a distinct gene pool, subspecific rank is suggested. The large stipules and the floral morphology clearly indicate the affinity to *L. montanus*.

MEXICO. CHIHUAHUA: Vic. of Chuchuichupa, summit of Sierra Madre, *Pringle 1206*(GH, F, G, K, ND-G, P, RSA, US), *1579*(P). Cerro Mohinora, 10 mi S of Guadalupe y Calvo, *Straw & Foreman 1943*(ENCB, MICH). DURANGO: Sierra Madre, 30 mi N of Guanaceví, *E. Nelson 4785*(US).

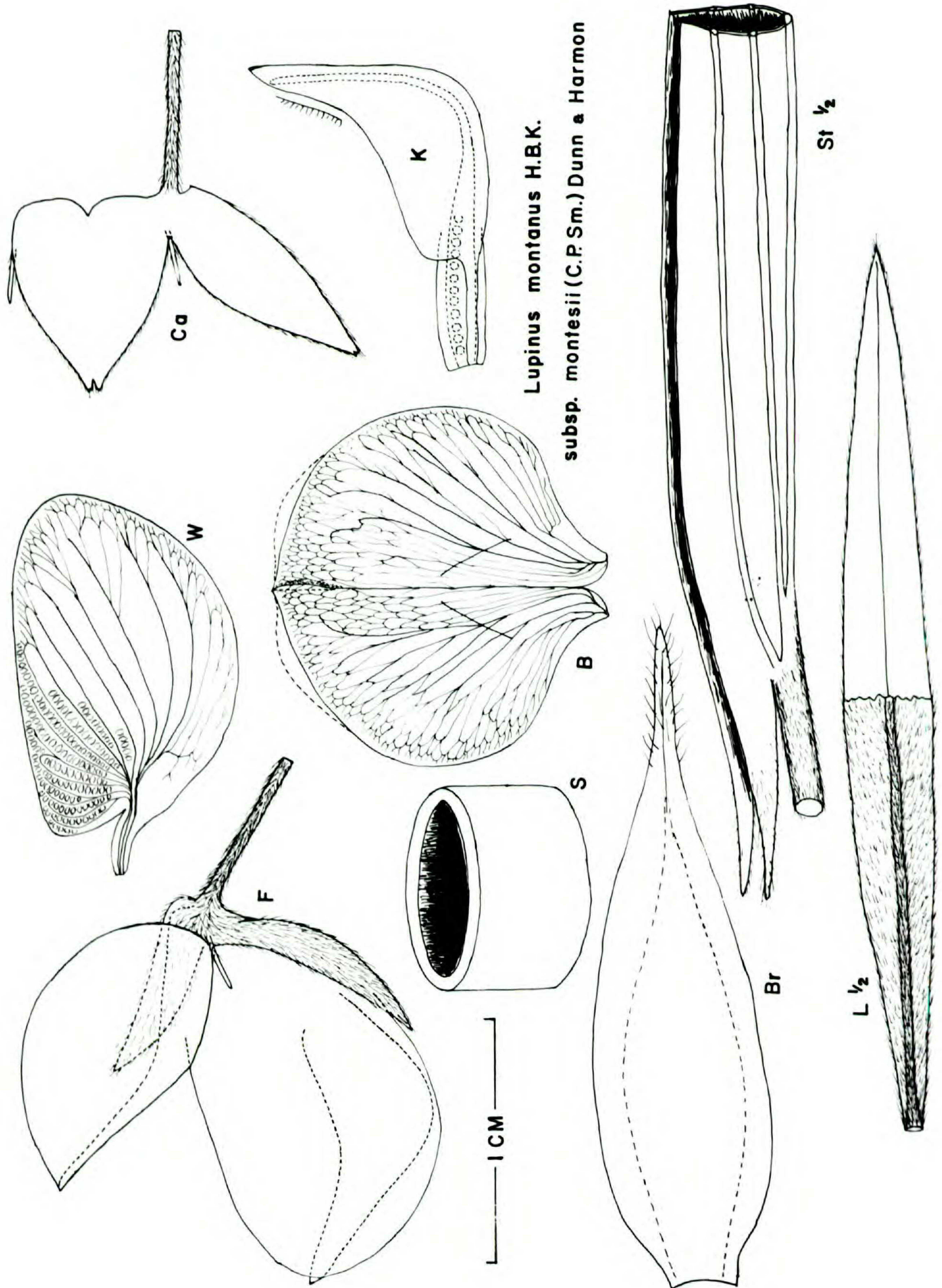
1e. *Lupinus montanus* subsp. *montesii* (C. P. Smith) Dunn & Harmon, comb nov.

L. montesii C. P. Smith, Sp. Lup. 41. 1938. TYPE: Mexico, Sinaloa, Cerro de San Rafael, San Ignacio, *Montes & Salazar 112*(US, holotype).—FIG. 5.

Plants perennial, from a woody caudex, 4–7 dm tall; stems hollow, glabrous below, sparsely strigose on the peduncle, rachis of raceme, and petioles, ligneous ridged, at least on drying, 6–8 mm in diameter; longest petioles 10–19 cm long, strigose on the portion not fused to the stipules; stipules sheathing and encircling $\frac{3}{4}$ of the stem, 4–10 cm long, the free, caudate tips 1–2 cm long, glabrous except for a few scattered setae near the tips; leaflets 9–14, linear-elliptic to narrowly elliptic, glabrous above, sparsely strigose below, the largest 6.5–9 cm long, 6–12 mm wide, acute-mucronate at the tips; peduncles hollow, 7–14 cm long, sparsely strigose; racemes verticillate to subverticillate, 20–35 cm long, rarely only 7 cm long in depauperate specimens, the rachis more densely strigose; bracts membranous, the long caudate tips with scattered setaceous hairs, caducous, 1.0–3.5 cm long, broad and completely covering the flower buds at the tip of the raceme, pedicels filamentous, 5–8.8 mm long, densely strigose; calyces appressed puberulent outside, glabrous within, the lower lip 8–12 mm long, generally entire, occasionally with a notch 0.1 mm deep, the upper lip 6–9.5 mm long, with an apical notch 0.3–1.6 mm deep, the base gibbous above, the lips connate 1.2–2 mm, a glabrous spatulate bracteole 1–4 mm long attached near the lip of the lateral sinuses; corollas blue and white, glabrous but the keel sometimes ciliate; banner 11.6–15.9 mm long, 12.5–17.4 mm wide, reflexed 6.4–7.7 mm, appressed 5.5–7.4 mm, reflexed/appressed ratio (average 1.17), banner angle 130° – 149° (average 141°); wings 13–18.4 mm long, 8.4–10.4 mm wide, the claw on the average 3.2 mm long; keel 3.8–5.2 mm wide in the middle, the angle 89° – 98° (average 91°), ciliate above near the acumen in half of the specimens, the others glabrous; ovules 10–13; only immature legumes seen, these strigose.

←

FIGURE 4. Structures of *Lupinus montanus* subsp. *glabrior* drawn to mean values, for the differences from subsp. *montanus*. All parts are drawn to the scale shown except the stipules and the leaflet which are drawn to half scale. The lettering is: B = banner, dorsal view; Br = bract; Ca = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)



Lupinus montanus H.B.K.
subsp. *montesii* (C.P. Sm.) Dunn & Harmon

The subspecies is known only from southwestern Durango, Mexico, in the general area of El Salto, and from Cerro de San Rafael, Sinaloa. Most of the collections have been west of El Salto but some have been cited as 45 miles to the south. The elevations have been near 7,000 ft, which is well below the normal altitude for *L. montanus*. The distribution is also geographically distinct from that of the species. Since the ecology, geography, morphology, and the composition of the alkaloids, are distinctive, it is suggested that there is a sufficiently distinct gene pool to recognize the taxon at the subspecific level. It is also distinct from subspecies *glabrior* in geography, morphology, and in chromatography. The large sheathing stipules and the floral morphology leave no doubt as to its affinity with *L. montanus*.

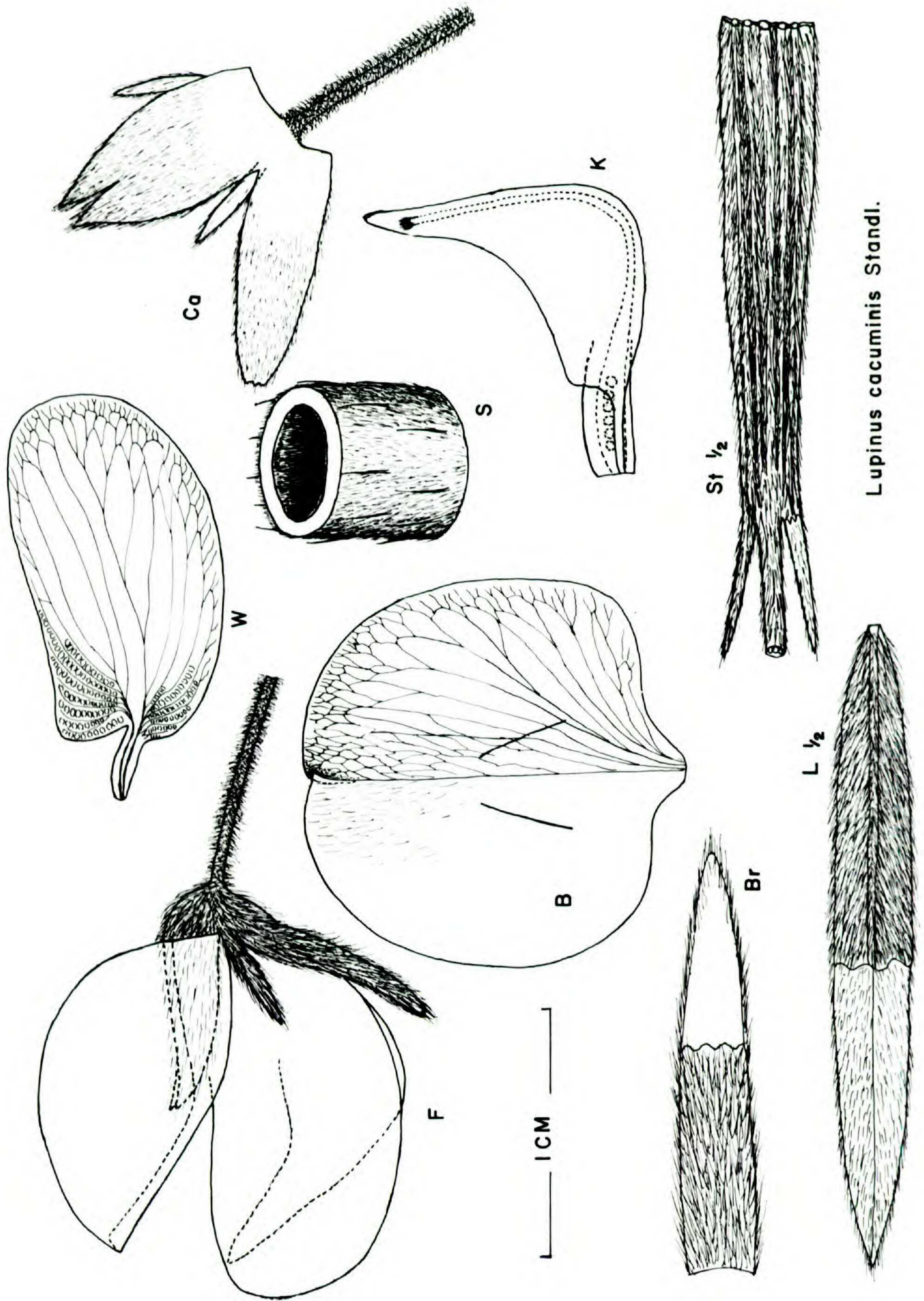
MEXICO. DURANGO: Cerro Auehueto, S of Huachichiles, *Maysvilles* 7258(MICH). Between Durango and Mazatlán, *Pennington* 242, 243(TEX). El Salto, *Guzman* in Sep. 1961 (ENCB). 20 km S of El Salto, *Gordon* 41(MICH, × *L. madrensis*). 19 mi SW of El Salto, *Waterfall* 15490(OKLA). 33 mi SW of El Salto, *Waterfall* 12714(OKLA, UMO). 3 mi W of La Ciudad, *LeDoux et al.* 2024(C, CAS, G, ENCB, K, MEX, MO, NY, U, UC, UMO, US). 6 mi W of La Ciudad, *Flyr* 274(TEX). 13 mi E of La Ciudad, *LeDoux et al.* 1996(ENCB, MEX, MO, NY, UMO, US). 8.4 mi W of La Ciudad, *Reveal & Atwood* 3507(MARY, UMO); *Breedlove* 18877(CAS, UMO). 14.3 mi NE of La Ciudad, *Pinkava et al.* 9495(ASU, UMO). 54 mi N of Estación Coyotes, *Breedlove* 18789(CAS, ENCB, UMO). Metates, N of Cueva, *Pennell* 18408(GH, US). Road to Pueblo Nuevo, *Maysvilles* 7760(MICH, × *L. madrensis*). W of Pueblo Nuevo, *Maysvilles* 8071(MICH, TEX). SINALOA: Cerro de San Rafael, San Ignacio, *Montes & Salazar* 112(US).

2. ***Lupinus cacuminus*** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 79. 1940. TYPE: Mexico, Nuevo León, peak of Cerro Potosí, Municipio de Galeana, *Mueller* 2269 (F, holotype; GH, MO, isotypes) [*Mueller* 1257 (F) labeled type in Standley's handwriting].—FIG. 6.

Plants perennial, caespitose, 3.5–6 dm tall; stems from a caudex, fistulose, the internodes between fully developed leaves only 1–3.5 cm long, pubescence all appressed-sericeous but of multiple hair types and lengths, the upper 2 or 3 nodes with branches initiated by anthesis of the primary racemes; largest petioles 5.5–13 cm long, reduced progressively upward, persistent long after the leaflets drop; stipules gradated from 4.5 cm long below to 1.5 cm above, imbricated below, connate 3 cm below to only 7–8 mm above, the free tips subulate-caudate; leaflets 10–14, linear-elliptic, appressed silky villous on both sides, sparsely above and the central area often glabrous, the largest 3–4 cm long, 3–4 mm wide (to 6 mm wide in a population on Peña Nevada), the tips acute and mucronate; peduncles 4–5 cm long, exceeded by the foliage; racemes 10–13 cm long but numerous bracts in a terminal tuft suggest that they may get much longer, the flowers tightly and spirally arranged; bracts lance-subulate, tardily deciduous or semipersistent; pedicels 6.5–12 mm long, hispidulous; calyces silky

←

FIGURE 5. Structures of *Lupinus montanus* subsp. *montesii* drawn to mean values, for the differences from subsp. *montanus*. All parts are drawn to the scale shown except those for the stipules and leaflet, which are drawn at half scale. The lettering is: B = banner, dorsal view; Br = bract; Ca = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)



white-villous with appressed hairs, the lower lip oblong-lanceolate, 8–10.2 mm long, tridentate or entire, the teeth 0.2–0.4 mm deep, the upper lip 7.7–10.4 mm long, bifid, the notch 1–4 mm deep, the lip oblong, 3.5–4 mm wide, flattened, the lips connate 1.4–2 mm, the bracteoles lanceolate, 1.5–6 mm long, attached at the lip of the lateral sinuses; banner sparsely pubescent dorsally on the distal portion, the tip emarginate, 14–17.5 mm long, 13–17.6 mm wide, reflexed 7–10 mm, appressed 6–8.5 mm, the angle 140° – 155° , the sulcus 1.5–1.8 mm deep midway; wings 15–17.4 mm long, 7–9.5 mm wide, the claw 2.5–3 mm long; keel 4–5 mm wide in the middle, glabrous or ciliate above near the acumen, the angle 80° – 90° at anthesis; ovules 5–7; pods 4–5 cm long, 9–11 mm wide, densely lanate with hairs 2 mm long.

While collectors have reported the plants as abundant in the upper pine woods and above timber line on Cerro Potosí, they have only been collected on three mountain peaks: Los Alpes, Cerro Potosí, and Peña Nevada. Flowering occurs from June through July and as late as August. The taxon appears intermediate between *L. montanus* and *L. muelleri* in several characteristics but has essentially the same spectrum of alkaloids as *L. montanus*. The specimens from Peña Nevada have sparse ciliation near the acumen of the keel.

MEXICO. COAHUILA: Los Alpes, 40 mi E of Saltillo, *Gentry et al.* 20059(UMO, US). NUEVO LEÓN: Cerro Potosí, Municipio de Galeana, *Mueller* 2269(F, GH, MICH, MO). Biol. Exp., U. of Ill., *Schneider* 958(F, GH, MICH, MO). Cerro Potosí, top of mt., *Beaman* 2654 (GH, MSC, US); *Gilbert* 26, 29(TEX); *Hinton* 17038(MICH). Cerro Potosí, near microwave tower, *Dunn et al.* 20203(F, K, MO, NY, RSA, UC, UMO, US); *Dziewanowski et al.* 1761(GH, ENCB, K, MEMO, MEX, MICH, MO, MSC, UMO, WUP); *MacGregor et al.* 314(KANU, UMO). 20 mi E of Galeana, *Mueller* 1257(F, GH, MICH, TEX). Peña Nevada, 26 mi NE of Dr. Arroyo, top of Picachio Onófre, *Beaman* 2690(GH, MSC, US). TAMAULIPAS: Peña Nevada, E and S slopes, *Stanford et al.* 2597(DAO, U, US). Summit of Peña Nevada, *G. Gillett* 1237(MSC).

3. ***Lupinus muelleri*** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 80. 1940. TYPE: Mexico, Nuevo León, Las Canoas, on Cerro Potosí, Municipio de Galeana, *Mueller* 2205 (F, holotype; CAS, GH, MICH, MO, TEX, isotypes).—FIG. 7.

Plants perennial; stems few to many from a woody caudex, woody with a solid pith, erect, 5–7 dm tall, 3 mm in diameter, branching from the upper nodes, thinly appressed strigose, with a cinereous undercoat of kinky hairs 0.2–0.4 mm long; petioles 1–2 cm long, filiform; stipules subulate to filiform, 6–8 mm long, connate to the petioles 2–4 mm; leaflets 6–8, the largest 2–2.5 cm long, elliptic-oblongate, the tip acute, mucronate, both surfaces densely strigose; peduncles 2.5–3.5 cm long; racemes 6–10 cm long, the flowers scattered to subverticillate; bracts subulate, 8–8.5 mm long, strigose outside; pedicels 7–11 mm long, with

←

FIGURE 6. Structures of *Lupinus cacuminus* drawn to the means values on the scale shown. The stipules and leaflet are drawn to half scale. The lettering is: B = banner, dorsal view; Br = bract; Ca = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)

hispidulous hairs 0.4 mm long; calyces sericeous outside, 2-lipped, the lower lip arcuate, boat shaped, 7.5–9 mm long, 3–4 mm wide, entire, or with teeth 0.2 mm long, the upper lip ovate, 7–7.4 mm long 3.8–4.5 mm wide toward the base, the apical notch 0.1–0.8 mm deep, the lips connate 1.2–1.4 mm, the bracteoles 0.8–2.0 mm long, linear, attached below the lateral sinus lips; banner sparsely pubescent dorsally near the distal portion, suborbicular, widest below the midpoint, reflexed 7.5–8.2 mm, appressed 6–7 mm, the angle 138° – 145° , the sulcus 1.5–1.8 mm deep, midway; wings glabrous, obovate, 13–15 mm long, 7–7.9 mm wide; keel ciliate above from the middle toward the acumen, 4–5 mm wide in the middle, the angle 83° – 88° ; ovules 6–8; pods 4–5 cm long, 10–12 mm wide, thinly subappressed kinky pilose, the hairs to 1 mm long; seeds 6.4 mm long, 5.7 mm wide, tan with faint mottling.

Thus far known only from Coahuila and Cerro Potosí in Nuevo León, where it was reported as abundant in pine woods, at elevations near 3,000 m. Flowering occurs from June to August.

MEXICO. COAHUILA: Puerto de la Siberio, Arteaga, *Marroquin 14*(MEMO). NUEVO LEÓN: Cerro Potosí, Las Canoas, Municipio de Galeana, *Mueller 2205*(CAS, F, GH, MICH, MO, TEX). Above Ejido, *Beaman 3311*(F, GH, ENCB, MSC, TEX); *Dunn et al. 20247*(UMO); *Dziewanowski et al. 1770*(CAS, G, ENCB, MO, NY, ORE, P, RSA, UC, UMO, US), *1771*(GH, ENCB, MEMO, MEX, MO, MSC, NY, RSA, SLP, UC, UMO, US, WUP).

4. *Lupinus kellermanianus* C. P. Smith, Sp. Lup. 90. 1938. TYPE: Guatemala, Volcán Agua, 9,000 ft, *Kellerman 4746* (US, holotype).—FIG. 8.

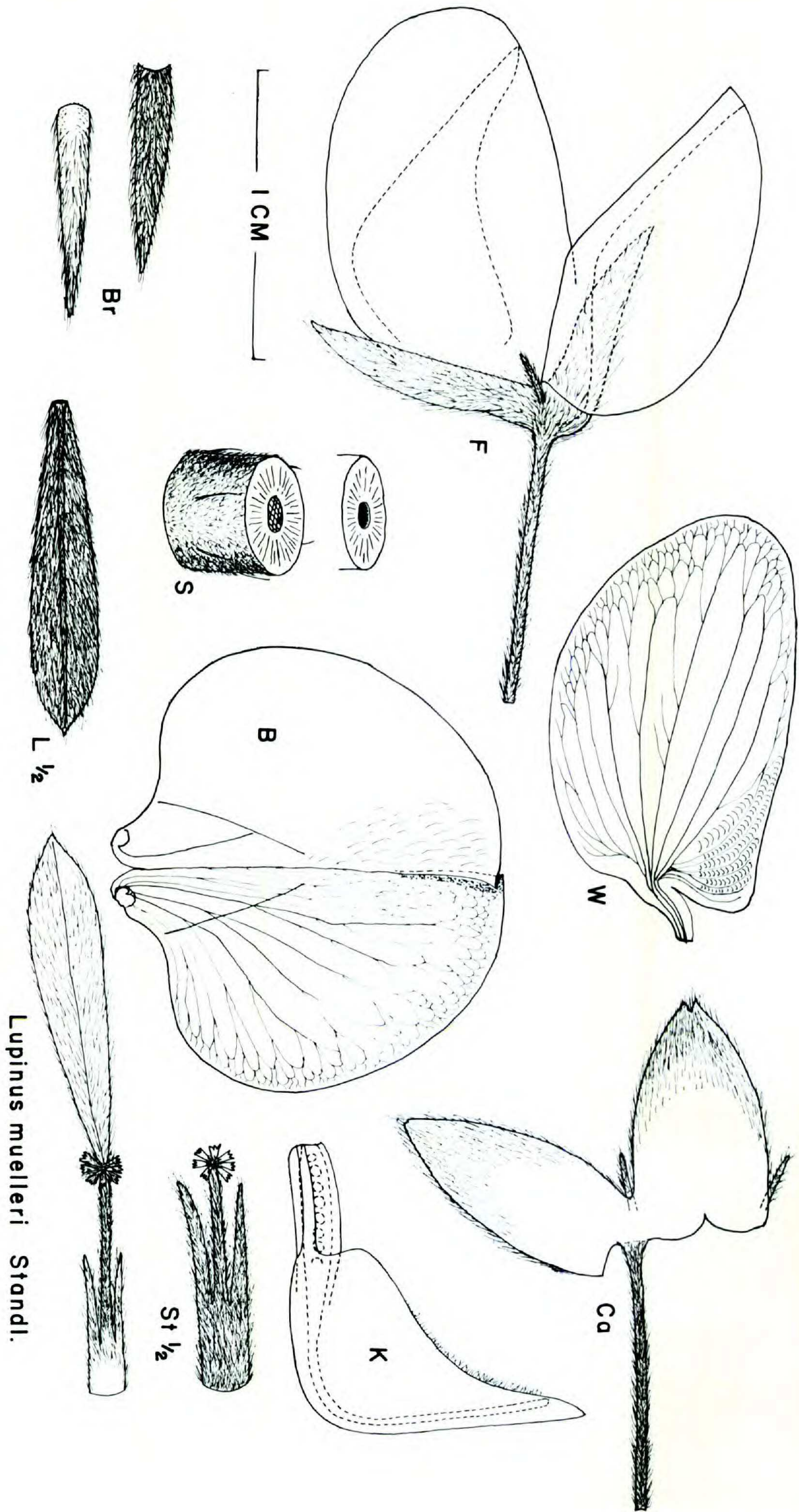
Plants perennial, shrubby; woody stems solid, the branches sometimes hollow, 3–6 mm in diameter, first year stems only 3 mm in diameter, strigose; petioles filiform, 2–4.5 cm long on the upper branches; stipules 8–18 mm long, the smallest at the base of the branches, the longest above, subulate-attenuate, connate 5–10 mm; leaflets 7–9, lanceolate, the tips acute, mucronate, the largest leaflets 2.5–3.5 cm long, 5 mm wide, sparsely kinky-villous above, canescent to kinky-villous below; peduncles 3 cm long at anthesis, 3–8 cm at fruiting; racemes 3–6 cm long, verticillate; bracts subulate-attenuate, 8–14 mm long, canescent; pedi-

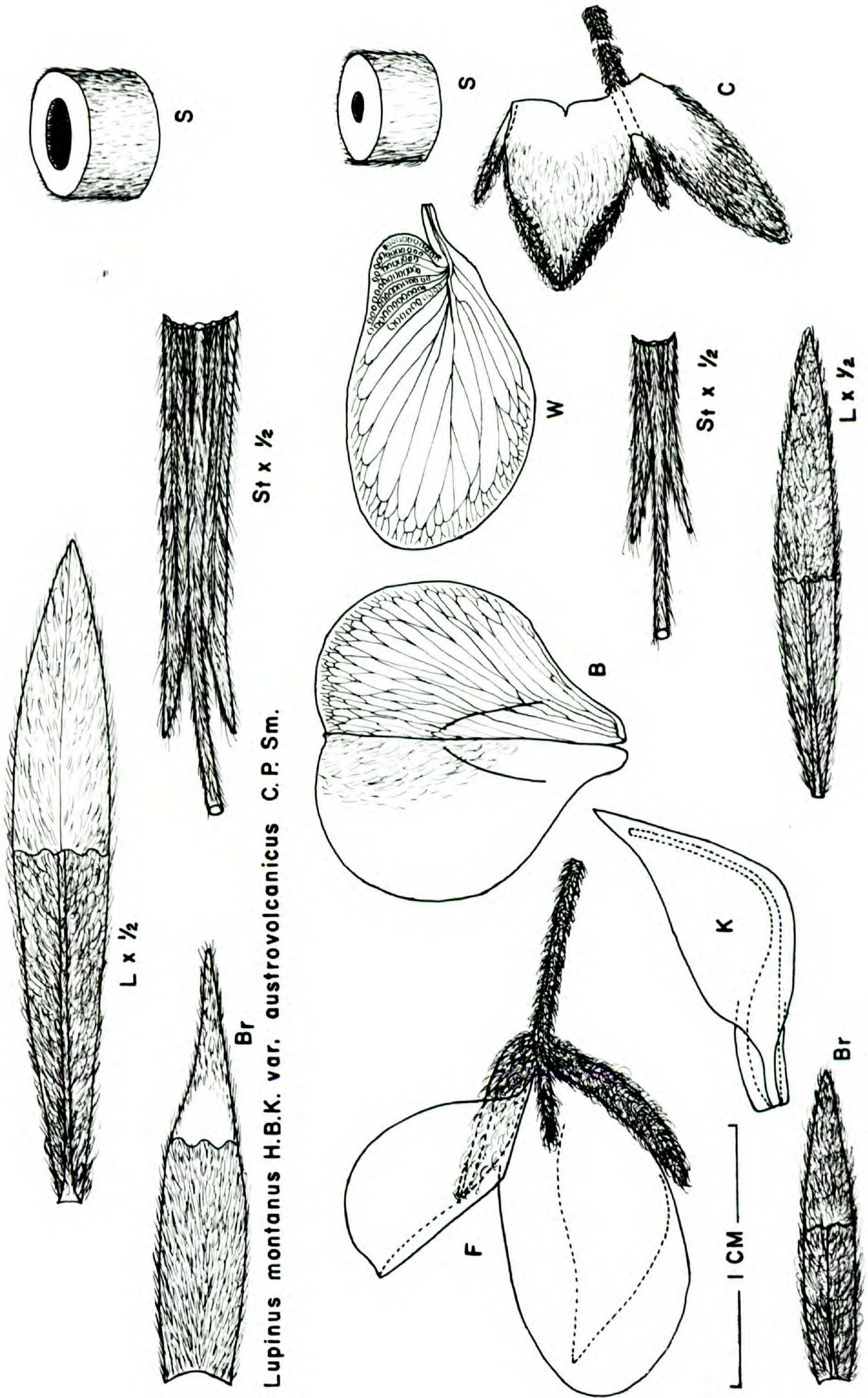
→

FIGURE 7. Structures of *Lupinus muelleri* drawn to the mean values on the scale shown, except the stipules and leaflet which are half scale. The lettering is: B = banner, dorsal view; Br = bract; Ca = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)

FIGURE 8. The vegetative structures for *Lupinus montanus* subsp. *montanus* var. *austrovolcanicus* are shown in the upper portion for comparison with *L. kellermanianus*. The stipules and leaflet are shown at half the scale. The floral traits are the same as shown for *L. montanus* subsp. *montanus* var. *montanus* in Fig. 2. The lower portions shows the structures of *L. kellermanianus* drawn to the mean values on the scale shown. The stipules and leaflet are drawn to half scale. The lettering is: B = banner, dorsal view; Br = bract; C = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)

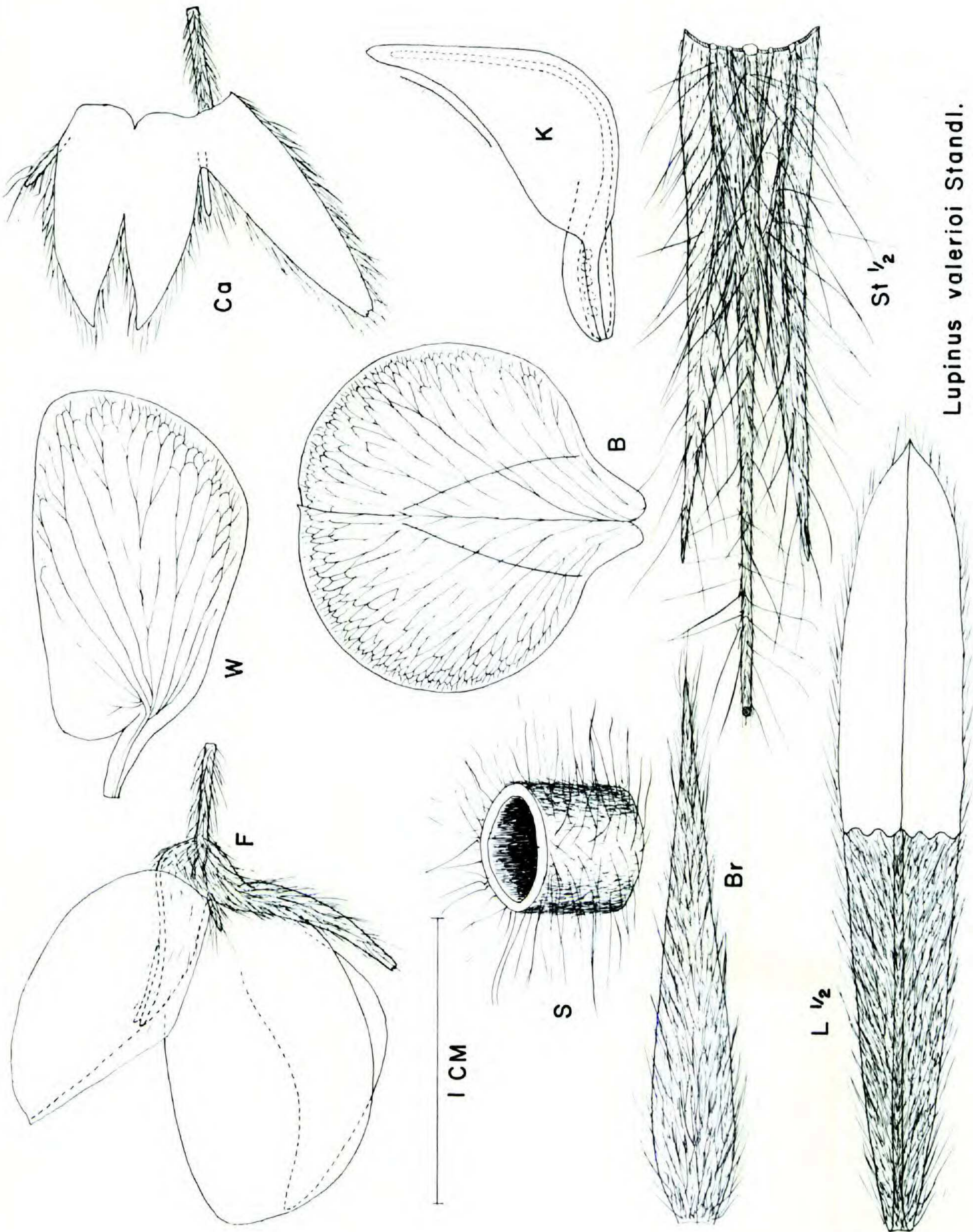
FIGURE 9. Structures of *Lupinus valerioi* drawn to the mean values at the scale shown, except the stipules and leaflet which are half scale. The lettering is: B = banner, dorsal view; Br = bract; Ca = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)





Lupinus montanus H.B.K. var. *austrovolcanicus* C.P. Sm.

Lupinus kellermanianus C.P. Sm.



Lupinus valerioi Standl.

cels 5 mm long at anthesis, 10–12 mm in fruit, hispidulous; calyces canescent, the lower lip 7.5–8.5 mm long, strigose within on the distal half, the upper lip 6.6–6.8 mm long, the notch 1.2–1.4 mm deep, the lips connate 1.5 mm laterally, the bracteoles lanceolate, 3–4 mm long, attached well below the lateral sinus lip on the side of the calyx cup or at the base; banner with a sparse patch of kinky hairs distally on the dorsal side, densest on the crest, obcordate to suborbicular, 12 mm long, 11.5–12 mm wide, reflexed near the midpoint; wings glabrous, 12–14 mm long; keel glabrous, 4–4.5 mm wide in the middle, the acumen very short; ovules 6–7; pods 3.5 cm long, 7 mm wide, sparsely pilose; seeds not available.

Very few collections have been made of this species known only from Volcán Agua and Zunil. The traits of the woody stems and pubescence on the banner have shown up on several neighboring peaks in plants which are otherwise typical *L. montanus*. This suggests introgression and the material named *L. montanus* var. *austrovolcanicus* is probably of hybrid derivation.

GUATEMALA. QUEZALTENANGO: Summit of Volcán Zunil, *Steyermark* 34848(F). SACATEPÉQUEZ: Volcán Agua, 9,000 ft, *Kellerman* 4746(US); *Kellerman* 15, 1905(US).

5. ***Lupinus valerioi*** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 545. 1937. TYPE: Costa Rica, San José, Cerro de las Vueltas, *Standley & Valerio* 43668 (holotype F).—FIG. 9.

Plants perennial, 6–9 dm tall, woody below; stems of current season hollow, subfistulose, to 5 mm in diameter, with abundant spreading pilose hairs 3–4 mm long, and with an undercoat of appressed strigose hairs; petioles of mature leaves, 6–12 cm long, pubescence as on the stems; stipules 2.5–4.5 cm long, connate to the petioles 1–2.5 cm, pilose, the free portion slender subulate-attenuate; leaflets 7–10, slenderly oblanceolate, the largest 4–7 cm long, 7–10 mm wide, glabrous above, subappressed strigose below; foliage dense from short internodes causing the lower stipules to be imbricated on the branches, 2–3 cm, with multiple leaves from the lateral buds of the upper nodes; peduncles 8–10 cm long; racemes 6–17 cm long, those of the branches shorter, verticillate to subverticillate, the whorls 10–25 mm distant in age; bracts caducous, lance-attenuate, 15–23 mm long, 2–3 mm wide in the lower portion of the raceme, with numerous pilose hairs 2–3 mm long dorsally; pedicels 3–4 mm long at anthesis, spreading pilose, the hairs 1–2 mm long; calyces densely subappressed pilose, the hairs 1–2.5 mm long, the lower lip 8.5–10.6 mm long, the tip bi- or trifid, the teeth 0.1–0.3 mm long, the upper lip 6–8.5 mm long, bifid, the notch 3.5–5.5 mm deep, the lips connate laterally 1.8–2.4 mm, the bracteoles 1.5–2.5 mm long, attached on the calyx cup below the lateral sinuses, with the lower portion fused to the calyx cup; banner glabrous, suborbicular, somewhat constricted below into a broad claw, 12–14 mm long, 11–12.5 mm wide, reflexed 5.5–6.5 mm, appressed 6.5–7 mm, reflexed/appressed ratio 0.76–0.83; wings 13.5–16.5 mm long, 6.5–8 mm wide, the claws 2.8–3.4 mm long; keels generally minutely ciliate above on the distal part, 3.5–4.5 mm wide in the middle, the angle 90°–95°; ovules 5; pods 3–3.5 cm long, 8.5–9.5 mm wide, densely villous, the hairs 2–3 mm long; seeds 4.5 mm long, 3 mm wide, dark brown to black.

The stipules and bracts show derivation from the *L. montanus* genome, which apparently was introduced and introgressed with a local taxon which at the present time appears to have dominated most of the characteristics, with only the vestige of traits from *L. montanus*. The flowering and fruiting materials have been collected from September through January at elevations from 2,700–3,100 m.

COSTA RICA. SAN JOSÉ: Cerro Chirripó, *Evans et al.* 118(MICH). Cerro Frio, *Jiménez* 2677(CR, F). Cerro Vueltas, *Standley & Valerio* 43668(F), 43974(F, US). Cord. Talamanca, *Weber* 6257(MICH).

LITERATURE CITED

- BEAMAN, J., D. C. D DE JONG & W. P. STOUTAMIRE. 1962. Chromosome studies in the alpine and subalpine floras of Mexico and Guatemala. *Amer. J. Bot.* 49: 41–50.
- CHO, Y. O. & R. O. MARTIN. 1971. Resolution and unambiguous identification of microgram amounts of 22 lupine alkaloids by sequential use of thin-layer and gas-liquid chromatography and mass spectrophotometry. *Anal. Biochem.* 44: 49–57.
- DUNN, D. B. 1972. *Lupinus mexicanus* Cerv. ex Lag. *Rhodora* 74: 489–494.
- HOLMGREN, P. K. & W. KEUKEN. 1974. *Index Herbariorum*. Ed. 6. *Regnum Veg.* 92: 1–397.
- HUMBOLDT, F. H. A. VON, A. J. A. BONPLAND & C. S. KUNTH. 1823. *Nova Genera et Species Plantarum*. Vol. 6. Paris.
- LAGASCA, M. 1816. *Genera Species Plantarum*. Madrid.
- NOWACKI, E. 1963. *Proc. XI Int. Congr. Genet.*, The Hague. Vol. 1: 246.
- & D. B. DUNN. 1964. Shrubby California lupines and relationships suggested by alkaloidal content. *Genet. Polon.* 5: 47–56.
- SHARMA, G. 1967. Cuticular variation in *Kalanchoe* and *Datura*. Ph.D. thesis, Univ. Missouri–Columbia, Columbia, Missouri.
- SMITH, C. P. 1948. Correlation-key to group 9, *montanus* complex. *Species lupinorum*. p. 608.